

A CONSPECTUS OF *MACHAERANTHERA* (ASTERACEAE: ASTEREAEE)

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ABSTRACT

A synopsis of *Machaeranthera* is presented with descriptions and keys where appropriate, synonymy, and discussion. The combination *Machaeranthera* subgenus *Sideranthus* (Nutt. ex Nees) R.L. Hartman is made. The following new sections or sectional combinations are recognized: *Machaeranthera* sections *Arida* R.L. Hartman, *Blepharodon* (DC.) R.L. Hartman, *Havardii* (R. Jackson) R.L. Hartman, *Sideranthus* (Nutt. ex Nees) R.L. Hartman, and *Stenoloba* R.L. Hartman. Other new combinations are: *Machaeranthera coloradoensis* (A. Gray) Osterh. var. *brandegei* (Rydb.) T.J. Watson ex R.L. Hartman, *M. viscida* (Wooton & Standley) R.L. Hartman, and *M. wigginsii* (S.F. Blake) R.L. Hartman. *Machaeranthera heterophylla* R.L. Hartman replaces *Haplopappus rhizomatus* M. Johnston which would become a later homonym if transferred to *Machaeranthera*.

KEY WORDS: Systematics, *Aster*, Asteraceae, Astereae, *Haplopappus*, *Machaeranthera*.

The preparation of the Asteraceae of México by B.L. Turner & G. Nesom has prompted publication of the conspectus of *Machaeranthera* from my dissertation (Hartman 1976) to make available several new combinations and a new name. All taxa are included except where otherwise noted. Subsequent (to 1976) modifications to the classification are indicated and recent references provided where appropriate. A detailed revision of *Machaeranthera* section *Blepharodon* with supporting data for the classification of the genus will be published separately.

MACHAERANTHERA

Machaeranthera Nees, *Gen. Sp. Aster.* p. 224. 1832. TYPE SPECIES: *Machaeranthera tanacetifolia* (Kunth) Nees (For complete synonymy see Turner 1987). BASIONYM: *Aster tanacetifolia* Kunth, *Nov. Gen. Sp.* 4:95. 1820.

Plants herbaceous, taprooted annuals, biennials, or perennials 0.3-11.0 dm tall, glabrous or variously pubescent, often with a much branched caudex. Leaves alternate, simple, linear to broadly lanceolate, spatulate, or triangular with entire, serrate, or dentate margins or oblong to ovate in outline with deeply pinnatifid to bipinnatifid margins, the teeth or lobes often bristle tipped. Heads radiate or eradiate. Involucre depressed hemispheric to turbinate, 0.4-2.5 cm wide. Phyllaries in 2-10, usually graduated series, imbricate, linear to broadly oblong or lanceolate, the lower portion usually stiff, stramineous or purple tinged, the upper fifth to four-fifths herbaceous, often purple tinged, or with a green strip or rhombic patch, erect, spreading, or reflexed, obtuse to long attenuate, often bristle tipped. Receptacle flat or slightly convex, usually alveolate, nearly smooth or with scales to 3 mm long subtending the florets. Ray florets when present pistillate, fertile, ca. 15-60, the corollas yellow, white, pink to purple, or blue, rounded to bi- or tridentate at the apex. Disc florets perfect, fertile, ca. 30-150 or more, the corollas yellow, 5-merous, with a cylindrical tube gradually flaring into the limb, with erect or spreading, triangular lobes. Style branches of ray florets stigmatic along the entire margin; disc florets stigmatic along the lower margins with appendages broadly triangular to attenuate. Achenes linear to broadly obovate or narrowly cordate, smooth to prominently ribbed, thin to thick walled, glabrous to densely pubescent; ray achenes terete to 3 sided or laterally flattened. Pappus persistent, often reduced or lacking on the ray florets, the bristles filiform to subulate, scabrous, white to brownish, in 1-3 often weakly graduated series, dorsiventrally flattened near the base in some species. Chromosome number, $n = 2, 3, 4, 5, 8, \text{ or } 9$.

Machaeranthera, as delimited in this treatment, may be separated from related genera by the following combinations of characters. The blue and white rayed members are distinguishable from *Aster* by being mostly taprooted and by having one or more of the following features: bristly tipped phyllaries and/or spiny toothed or pinnatifid leaves; epappose ray florets; or linear to clavate achenes 3-6 mm long. They are most easily separated from *Xylorhiza* in that the taproot is not massive with copious periderm (Watson 1977). The yellow rayed members may be distinguished from related homochromous genera by the short, turbinate achenes (less than 3 mm long) and the gradually flaring (vs. abruptly dilated) disc corollas.

Key to the Subgenera and Sections of *Machaeranthera*

1. Ray florets white (sometimes yellowish when dry), pink, or purple (yellow in *M. heterophylla*, section *Blepharodon*, which grows in loose clumps with stems arising from short rhizomes, 2-3 mm thick, attached to a woody rootstock; W Nuevo León, México) or the heads eradiate (subgenus *Machaeranthera*) 2.
2. Pappus absent from ray florets, or if heads eradiate (*M. carnosa*) then flowering stems glabrous and glaucous, heads turbinate, and achenes oblong-fusiform, thin walled with 18-22 filiform nerves . 3.
 3. Phyllaries in 2-3(-4) series of often nearly equal length, linear to lanceolate, 4-8 times as long as wide, the apices narrowly acute to acuminate; leaves on upper half of plant usually with entire margins; restricted mostly to grasslands or forests Section 5. *Psilactis*
 - 3' Phyllaries in (3-)4-8 graduated series, broadly oblong, usually 2-4 times as long as wide, the apices broadly acute; leaves on the upper half of plant usually serrate to deeply lobed (often entire in *M. coulteri* from SW Sonora, México); restricted usually to desert regions Section 4. *Arida*
- 2' Pappus present on ray florets (often greatly reduced), or if heads eradiate (three species, section *Blepharodon*) then flowering stems pubescent, heads hemispheric to campanulate, and achenes broadly oblong to obovoid, thick walled with 6-16 wide ribs 4.
 4. Achenes 3-6 mm long, the walls thin, flexible, smooth or obscurely nerved, glabrous to sparingly pubescent; pappus 5-8 mm long; leaves never pinnatifid; ray florets always present Section 3. *Hesperastrum*
 - 4' Achenes 1.0-3.5 mm long, if greater than 2.5 mm long then the walls thick and bony, prominently nerved or ribbed, and moderately to densely pubescent; pappus 0.3-8.0 mm long; leaves often pinnatifid to deeply bipinnatifid; ray florets absent in some species 5.
 5. Plants perennial with branching caudices (*Machaeranthera gymnocephala* taprooted, sometimes biennial, root crown little branched); pappus 3.5-8.0 mm long; receptacle with scales 0.3-1.5 mm long; leaves rarely pinnatifid, if with serrate or dentate margins the teeth usually tipped by bristles 1-4 mm long; ray florets absent in three species Section 2. *Blepharodon*

- 5' Plants taprooted annuals or short lived perennials (forming vegetative rosettes in *Aster blepharophyllus*); pappus 1.0-6.5 mm long; receptacle naked or essentially so; leaves often pinnatifid or bipinnatifid, if with toothed margins the teeth not terminated by prominent bristles (essentially entire with 8-20 prominent cilia, 0.4-0.8(-1.5) mm long, per side in *A. blepharophyllus*); ray florets present 6.
6. Leaves entire to lacinate, if deeply pinnatifid (*Machaeranthera arida*, *M. parviflora*) or bipinnatifid (*M. turneri*) then those on the upper parts of the stems less than 1.5 cm long with usually entire lobes; pappus of disc florets 2.5-4.5(-5.0) mm long; achenes thin walled with filiform nerves Section 4. *Arida*
- 6' Leaves deeply pinnatifid or more commonly bipinnatifid with irregularly toothed lobes, usually not markedly reduced above; pappus of disc florets 4.5-6.5 mm long; achenes thick walled with pronounced nerves or ribs Section 1. *Machaeranthera*
- 1' Ray florets yellow, always present; (rhizomes absent) (Subgenus *Sideranthus*) 7.
7. Achenes of disc florets broadly obovate to obscurely and narrowly cordate, the thick, bony walls with 10-12 prominent ribs, densely pubescent, the margins thickened; pappus 2-3 mm long, mostly of subulate, markedly dorsiventrally flattened bristles; plants annual; leaves deeply pinnatifid or bipinnatifid; restricted to the mountains of SW Chihuahua, México Section 8. *Stenoloba*
- 7' Achenes of disc florets oblong to narrowly obovate, the usually thin, flexible walls smooth or with 6-16 obscure ribs, glabrous to moderately pubescent, the margins not thickened; pappus 3.5-7.0 mm long, of filiform, only slightly flattened bristles; plants annual to perennial; leaves entire to bipinnatifid; occurring elsewhere 8.
8. Plants taprooted annuals; phyllaries obtuse to broadly acute, not bristle tipped; leaves serrate or dentate, the teeth blunt or terminating in a stiff callosity, not bristle tipped; achenes oblong or narrowly elliptic with 12-14 barely discernible nerves, sparsely pubescent; restricted to the lowlands of SE New Mexico and W Texas Section 7. *Havardii*
- 8' Plants perennials with much branched caudices, if taprooted annuals then phyllaries with narrowly acute to acuminate and prominently bristle tipped apices; leaves various, if serrate or dentate, the teeth bristle tipped; achenes elliptic to narrowly

obovate with 6-16 weak ribs, glabrous to moderately pubescent; widely distributed from Canada S to central México and the Cape region of Baja California Sur and adjacent islands Section 6. *Sideranthus*

MACHAERANTHERA Subgenus *MACHAERANTHERA* (Sections 1-5)

1. *Machaeranthera* subgenus *Machaeranthera*. (For complete synonymy see Turner 1987.)

Ray florets white (sometimes yellowish when dry), pink, or purple (yellow in *Machaeranthera heterophylla*, section *Blepharodon*) or the heads eradiate.

1. *Machaeranthera* section *Machaeranthera*. (For complete synonymy see Turner 1987.)

Plants taprooted annuals or biennials, 1-4 dm tall. Leaves deeply pinnatifid to bipinnatifid. Heads radiate. Involucre hemispheric to turbinate. Phyllaries in 4-7 graduated series, narrowly to broadly linear, the lower portion rigid, stramineous, with a midline, the upper fourth to three-fourths green, usually densely stipitate glandular, erect or more commonly widely divergent to reflexed, acute though usually abruptly acuminate to long attenuate. Receptacles alveolate with poorly developed scales. Ray florets usually intensely violet blue. Achenes slightly dimorphic, 2.4-3.2 mm long, narrowly obovate, flattened laterally, the walls moderately thick with 8-18 pronounced nerves or ribs, moderately pubescent; ray achenes rounded dorsally. Pappus similar in ray and disc florets, 4.5-6.5 mm long, white or tawny, the bristles filiform, not basally flattened, in 2-3 poorly defined series. Chromosome number, $n = 4$.

This section contains two species, both excellently treated by Turner (1987).

Machaeranthera tanacetifolia (Kunth) Nees, *Gen. Sp. Aster.* p. 225. 1832.

Machaeranthera tagetina E. Greene, *Pittonia* 4:71. 1899.

2. *Machaeranthera* section *Blepharodon* (DC.) R.L. Hartman, *comb. nov.* BASIONYM: *Haplopappus* section *Blepharodon* DC., *Prodr.* 5:346. 1836. TYPE SPECIES: *Aplopappus gymnocephalus* DC., *Prodr.* 5:346. 1836 (\equiv *Machaeranthera gymnocephala* [DC.] Shinn.).

Eriocarpum Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:320. 1840.

TYPE SPECIES: *Eriocarpum grindelioides* Nutt. (\equiv *Machaeranthera grindelioides* [Nutt.] Shinn.). *Haplopappus* section *Eriocarpaea* Benth. & Hook., *Gen. Pl.* 2:254. 1873, based on *Eriocarpum* Nutt.

Machaeranthera series *Originales* Cronq. & Keck, *Brittonia* 9:237. 1957.

TYPE SPECIES: *Machaeranthera blephariphylla* (A. Gray) Shinn.

Plants taprooted annuals, biennials, or perennials, 0.3-5.0 dm tall, often with a much branched caudex or in loose clumps with several short rhizomes, 2-3 mm thick, arising from a woody rootstock. Leaves serrate or dentate, the teeth usually bristle tipped, but entire or rarely pinnatifid in a few species. Heads radiate or eradiate. Involucre depressed hemispheric to campanulate. Phyllaries in 3-6 graduated series, linear to lanceolate, the lower portion thickened, stramineous, the upper half to one-fourth herbaceous or with a green or purple tinged strip or patch, stipitate glandular to canescent, erect to reflexed, obtuse to long attenuate and usually bristle tipped. Receptacle alveolate, with often lacerate scales 0.3-1.5 mm long. Ray florets white, pink, purple, or lavender when present (yellow in *Machaeranthera heterophylla*). Achenes slightly dimorphic, (1.0-)1.5-3.5 mm long, narrowly obovoid to oblong, the walls thick with 6-18, often prominent ribs, usually densely pubescent; ray achenes obscurely 3 sided; disc achenes compressed laterally. Pappus usually 3.5-8.0 mm long, white to tawny, the bristles dorsiventrally flattened basally, in 2-4 graduated series, the pappus of the ray florets often much reduced in size. Chromosome number, $n = 4$ or 8.

Section *Blepharodon* corresponds to series *Originales* of Cronquist & Keck (1957), a group to which they referred four species and one variety all of which I retain in section *Blepharodon*.

A key to the species of this section, full synonymy, species descriptions, geographical distributions, and detailed discussion of the phylogeny will be published separately.

Machaeranthera blephariphylla (A. Gray) Shinn., *Field & Lab.* 18:38. 1950.

Machaeranthera coloradoensis (A. Gray) Osterh., *Torrey* 27:64. 1927.
var. *coloradoensis*.

Machaeranthera coloradoensis (A. Gray) Osterh. var. *brandegei* (Rydb.) T.J. Watson ex R.L. Hartman, *comb. nov.* BASIONYM: *Xylorhiza brandegei* Rydb., *Bull. Torrey Bot. Club* 32:124. 1905, non *Aplopappus brandegei* A. Gray, *Syn. Fl. N. Amer.* 1(2):132. 1884. TYPE: U.S.A. Colorado: San Juan Pass [may refer to area now known as Spring Creek Pass, W.A. Weber, pers. comm.], 1875, *T.S. Brandegei 1165* (HOLOTYPE: GH; Isotypes: NY!, UC!).

- Machaeranthera crutchfieldii* B. Turner, *Phytologia* 26:116. 1973.
- Machaeranthera grindelioides* (Nutt.) Shinn., *Field & Lab.* 18:40. 1950.
var. *grindelioides*.
- Machaeranthera grindelioides* (Nutt.) Shinn. var. *depressa* (Maguire)
Cronq. & Keck, *Brittonia* 9:237. 1957.
- Machaeranthera gymnocephala* (DC.) Shinn., *Field & Lab.* 18:40. 1950.
- Machaeranthera gypsophila* B. Turner, *Phytologia* 26:117. 1973.
- Machaeranthera heterophylla* R.L. Hartman, *nom. nov.* Based on
Haplopappus rhizomatus M. Johnston, *Rhodora* 63:177. 1961, non
Machaeranthera rhizomata Nelson & J.F. Macbr., *Bot. Gaz.* (Craw-
fordsville) 62:148. 1916. TYPE: MÉXICO. Nuevo León: Saltillo-
Matehuala hwy., 8 km N of jct. of the side road to Galeana, 8 Oct
1959, *J. Graham & M.C. Johnston 4203* (HOLOTYPE: TEX!).

This species was placed in section *Sideranthus* by Hartman (1976) largely because of the yellow ray florets (vs. white, pink, purple, or lavender, when present, in section *Blepharodon*). According to Ray Jackson (pers. comm.; Bundrant 1987), *Machaeranthera heterophylla* crosses readily with members of section *Blepharodon* and the offspring have high seed set and meiotic regularity indicating the lack of major structural differentiation. After a re-evaluation of the fruit and vegetative morphology, I concur with Jackson on its placement in section *Blepharodon*.

- Machaeranthera johnstonii* (S.F. Blake) B. Turner, *Amer. J. Bot.* 60:837.
1973.
- Machaeranthera restiformis* B. Turner, *Amer. J. Bot.* 60:836, f. 1-5.
1973.

3. *Machaeranthera* section *Hesperastrum* A. Gray, *Proc. Amer. Acad. Arts* 6:539. 1865. TYPE SPECIES: *Machaeranthera shastensis* A. Gray, *Proc. Amer. Acad. Arts* 6:539. 1865. (\equiv *Machaeranthera canescens* [Pursh] A. Gray var. *shastensis* [A. Gray] B. Turner) (For complete synonymy see Turner 1987).

Plants taprooted annuals to short lived perennials, 0.2-10.0 dm tall. Leaves entire to coarsely serrate or dentate, the teeth bristle tipped in a few species. Heads radiate. Involucre turbinate to depressed hemispheric. Phyllaries in 3-10 graduated series, linear subulate to broadly oblong, lower portion usually thickened, stramineous, upper third to two-thirds green, or purple tinged, cinereous to densely stipitate glandular, erect to reflexed, obtuse to acuminate or long attenuate, not prominently bristle tipped. Receptacles alveolate, with

poorly developed scales mostly less than 0.3 mm long. Ray florets white to dark blue or purple. Achenes monomorphic, mostly 3-6 mm long, linear to clavate, often asymmetrical, often markedly flattened laterally, walls thin, smooth or obscurely nerved, glabrous to sparingly pubescent. Pappus similar in ray and disc florets, mostly 5-8 mm long, white or tawny, bristles filiform, not basally flattened, in 2-3 poorly defined series. Chromosome number, $n = 4$ (or 5, but probably based on erroneous counts; see Turner 1987).

In the reconstitution of *Machaeranthera* by Cronquist & Keck (1957), members of this section were treated in series *Variabiles*. I made no attempt to provide a taxonomic treatment of this extremely complex section (Hartman 1976). An excellent revision was published by Turner (1987) to which the reader is referred. He recognized 16 varieties distributed among three species as opposed to 11 species and 5 varieties listed by Cronquist & Keck.

4. *Machaeranthera* section *Arida* R.L. Hartman, *sect. nov.* TYPE SPECIES: *Machaeranthera arida* B. Turner & D. Horne.

Machaeranthera section *Psilactis* affinis sed phyllariis 4-6 seriatis inaequalibus late oblongis saepe 2-4-plo longioribus quam latoribus, apicibus late acutis et foliis saepe serratis vel profunde pinnatisectis differt.

Taprooted annuals or rarely short lived perennials, 1-4(-10) dm tall (rhizomatous, forming vegetative rosettes in *Aster blepharophyllus*). Leaves entire, dentate, lacerate to deeply pinnatifid or bipinnatifid. Heads usually radiate. Involucre depressed hemispheric to turbinate. Phyllaries in 4-8 graduated series, broadly oblong to lanceolate, lower portion usually stramineous, often with a midline, upper third to half dark green to purple tinged, often densely stipitate glandular, usually erect or occasionally spreading to reflexed, usually obtuse to broadly acute, or in inner series often acuminate, not bristle tipped. Receptacle indistinctly alveolate, naked or essentially so. Ray florets light to dark blue (absent from *Machaeranthera carnosus*). Achenes monomorphic, 1.5-2.8(-3.2) mm long, narrowly oblong, only slightly compressed laterally, the walls thin with 10-22 filiform nerves, moderately to densely pubescent. Pappus of disc florets 2.5-4.5(-5.0) mm long, white, bristles filiform, not basally flattened or only slightly so, in 2-3 poorly defined series, those of ray florets well developed or lacking. Chromosome number, $n = 5$.

Three members of section *Arida* traditionally have been placed in *Psilactis* A. Gray. Turner & Horne (1964) reduced *Psilactis* to a section of *Machaeranthera*, in part because the diagnostic feature of *Psilactis*, i.e. absence of a pappus on ray florets, segregated in a Mendelian fashion in *M. coulteri*. Furthermore, they noted the strong morphological resemblance of *M. coulteri* and *M. arida* to *M. parviflora*, a taxon which was placed with *M. tanacetifolia* and *M. tagetina* in series *Verae* by Cronquist & Keck (1957). *Machaeranthera*

parviflora, which constitutes my fourth member of section *Arida*, would not have been placed in what had been the genus *Psilactis*, because of the pappus on ray florets. Interestingly, plants of this species from Valencia and Bernalillo counties, New Mexico, N and W to SW Colorado, SE Utah, and E Arizona have epappose rays.

The four species placed in section *Arida* are diploid with a chromosomal base of $x = 5$, synthesize 7-O-glycosides of apigenin and luteolin as leaf flavonoids, and have phyllaries in 4-6 graduated series, broadly oblong; and dark green to purple tinged in upper third to half. The five members retained in section *Psilactis* are diploid with chromosome numbers of $n = 3, 4, \text{ or } 9$, synthesize 3-O-glycosides of kaempferol and quercetin, and have phyllaries in 2-3 series of nearly equal length or somewhat graduated, linear to narrowly lanceolate, green, and herbaceous throughout (Hartman 1976).

The following key is based in part on data in Turner (1986) and Nesom (1990).

1. Ray achenes with prominent pappus (heads eradiate in *M. carnos*a) .. 2.
 2. Leaves entire to toothed 3.
 3. Heads eradiate *M. carnos*a
 - 3' Heads radiate 4.
 4. Plants annual; leaf margin entire and glabrous or with 1-8 teeth/side, each spinulose tipped; involucre hemispheric, 10-16 mm wide; phyllaries linear lanceolate to oblong lanceolate, narrowly acute to acuminate or attenuate *M. riparia*
 - 4' Plants perennial, rhizomatous, forming vegetative rosettes; leaf margin essentially entire with 8-20 prominent cilia/side; involucre turbinate, 5-8 mm wide; phyllaries oblong ovate to obovate, broadly acute to short acuminate *Aster blepharophyllus*
 - 2' Leaves, at least some, pinnatifid to bipinnatifid 5.
 5. Receptacle diameter 8-11 mm; phyllary tips spreading to reflexed *M. turneri*
 - 5' Receptacle diameter 2-7 mm; phyllary tips mostly appressed *M. parviflora*
- 1' Ray achenes epappose (except in occasional plants) 6.
 6. Mid-stems essentially glabrous or with few sessile glands 7.
 7. Leaves deeply pinnatifid; restricted to SW Colorado, N New Mexico, SE Utah, and E Arizona *M. parviflora*

- 7' Leaves entire or toothed; restricted to SW Sonora,
México *M. coulteri*
- 6' Mid-stems densely glandular pubescent 8.
8. Involucre 3-6 mm high, 5-10 mm wide; mid-stems densely glandular, also with longer, crisp, eglandular trichomes interspersed; occurring in S Nevada, S California, S Arizona, and N Sonora, México *M. arida*
- 8' Involucre 6-8 mm high, 10-15 mm wide; mid-stems glandular, eglandular trichomes none; occurring in N Baja California Sur and adjacent W Sonora *M. crispa*

Machaeranthera arida B. Turner & D. Horne, *Brittonia* 16:324. 1964.
TYPE: U.S.A. California: San Bernardino Co., Mesquite Valley, 2.8 km SW of Kingston, 15 May 1941, *C.B. Wolf 10695* (HOLOTYPE: DS!; Isotypes: NY!, TEX!, UC).

Machaeranthera arizonica R. Jackson & R. Johnson, *Rhodora* 69: 476, f. 1. 1967. TYPE: U.S.A. Arizona: Pima Co., low, rocky hillsides and sandy soil around Quitobaquito Springs, 31 Mar 1962, *R.C. Jackson & R.R. Johnson 3043-1* (HOLOTYPE: KANU!; Isotypes: ARIZ, KANU! [2 sheets]).

Machaeranthera ammophila Rev., *Bull. Torrey Bot. Club* 97:172. 1970. TYPE: U.S.A. Nevada: Nye Co., on the W edge of Ash Meadows, 0.5 km W of Carson Slough, 21 Aug 1968, *J.L. Reveal & N.H. Holmgren 1882* (HOLOTYPE: US!; Isotypes: GH!, NY! [2 sheets]).

Machaeranthera arizonica was based on specimens from Quitobaquito Springs, Arizona which had been treated under *M. arida* (Turner & Horne 1964). The two species were said to differ in a number of quantitative features of ray and disc florets (Jackson & Johnson 1967), but overlap of statistical ranges for measurements is considerable for nearly all the characters. Consequently, separation of the two would require calculation of statistical means. Since delimitation of taxa is based on morphological gaps, not statistical means, this is a very unrealistic approach in systematics. Further, since other collections from the type locality of *M. arizonica* are essentially identical to *M. arida*, the two are here considered conspecific.

According to Ray Jackson (pers. comm.), "the type of *M. arizonica* is a woody-based perennial" [which is true] "found on a rocky area about the hillside origin of Quitobaquito Springs," and

"the last time I was there, new parking lot construction had apparently introduced what appeared to be *M. arida* around the parking lot and catchment pound below." This may be the case. Alternatively, after studying a number of specimens of *M. arida* from the vicinity of the Springs and elsewhere, I hypothesize the following. In this portion of the geographical range, this taxon may become perennial and even have a woody taproot. Upon germination and during initial flowering, usually in March, the leaves, especially on the lower half of the plant, are finely pinnatifid and mostly 1.5-4.0 cm long. With time and favorable growing conditions the leaves which persist, or those on subsequent growth, are merely toothed, xerophytic in adaptation, and mostly 0.3-1.2 cm long. One plant (Hartman & Chiang C. 4366; RM) of *M. arida* which was cultivated for two seasons at the Desert Botanical Garden, Phoenix, Arizona, with only occasional watering, made this transition.

Reveal & Cronquist (Reveal 1970) considered *Machaeranthera ammophila* to be a member of series *Variabiles* (\equiv section *Hesperastrum*) and most closely allied to *M. leucanthemifolia*, even though it keys to *M. parviflora* of series *Verae* (here treated in section *Arida*) in the revision of *Machaeranthera* by Cronquist & Keck (1957). I have examined the type material and find that it differs in no important features from *M. arida* and therefore consider them conspecific. Apparently, Reveal & Cronquist failed to note the epappose ray florets which are characteristic of most members of this section and of section *Psilactis*.

Machaeranthera coulteri (A. Gray) B. Turner & D. Horne, *Brittonia* 16:322. 1964. BASIONYM: *Psilactis coulteri* A. Gray, *Mem. Amer. Acad. Arts*, ser. 2, 4:72. 1849. TYPE: MÉXICO. Sonora: probably the vicinity of Guaymas, *T. Coulter 295* (HOLOTYPE: GH!).

Machaeranthera crispa (Brandege) B. Turner & D. Horne, *Brittonia* 16:321. 1964. BASIONYM: *Psilactis crispa* Brandege, *Proc. Calif. Acad. Sci.*, ser. 2, 2:169. 1889. TYPE: MÉXICO. Baja California Sur: "alkaline soil, San Joaquin, San Ignacio," 1 Apr 1889, *T.S. Brandegee s.n.* (HOLOTYPE: UC; Isotypes: GH!, PH [photo, RM!], US!).

This species was thought to be restricted to the N half of Baja California Sur, but it is common in W Sonora, México (Hartman 1976). Many of these collections were interpreted by Turner (1986) as intermediates between *Machaeranthera coulteri* and *M. arida*. Based on my circumscription of the taxa, *Machaeranthera arida*

occurs in S Nevada, S Arizona, S California and N Sonora, México, S to near El Desemboque. In Sonora. *M. crisper* ranges in a strip 10-30 km wide from the vicinity of Bahía Kino to about 60 km SE of Guaymas. The geographical separation of the two taxa, as currently documented, is approximately 100 km. *Machaeranthera coulteri* is found in an area from 50 km N to 55 km SE of Guaymas and is sympatric with *M. crisper*.

From the material studied by Turner (1986 and subsequently) justifying the transfer of *Machaeranthera arida* to a variety of *M. coulteri* because of putative hybridization between the two, 19 sheets were sent for re-evaluation of my taxonomic treatment. Two were *M. coulteri* (in agreement with annotations by Turner), eight were *M. arida* (also in agreement), but nine were *M. crisper* as I define it. This last group was annotated by Professor Turner as *M. coulteri* vars. *coulteri* (2 sheets) or *arida* (2 sheets) or as intermediates (4 sheets). Four of these (Hartman, et al. 3517, LL, as *M. coulteri* var. *arida*; Hartman, et al. 3516, 2 sheets, LL, as intermediate; Powell & Averett 1524, LL, intermediate) are very similar in leaf morphology and other features to specimens of *M. crisper* from Baja California Sur and I am convinced that they are conspecific. The other specimens which I place in *M. crisper* have leaves which appear to be adapted to more xerophytic conditions (thicker texture, more uniformly toothed, reduced size). Some are from the vicinity of the good *M. crisper* mentioned above, while the remainder were collected near Guaymas. As I believe is true of *M. arida*, I hypothesize that due to yearly fluctuations in precipitation, the variation is due to phenotypic plasticity.

Machaeranthera parviflora A. Gray, *Pl. Wright*. 1:90. 1852. TYPE: U.S.A. Texas: "collected in expedition from W Texas to El Paso, N. Mex.," May-Oct 1849, *C. Wright* 271 (HOLOTYPE: GH!; Isotypes: NY!, US [photo, RM!]). *Aster parviflorus* (A. Gray) A. Gray in W.H. Brewer & S. Watson, *Bot. California* 1:322. 1876, non Nees, *Syn. Aster. Herb.* p. 29. 1818, nec. Darl., *Fl. Cestr.* p. 446. 1826. *Aster parvulus* S.F. Blake in Tidestrom, *Contr. U.S. Natl. Herb.* 25:563. 1925, based on *Machaeranthera parviflora* A. Gray.

Machaeranthera tanacetifolia (Kunth) Nees var. *pygmaea* A. Gray, *Pl. Wright*. 2:74. 1853. TYPE: U.S.A. New Mexico: near El Paso, 1851, *C. Wright* 1395 (HOLOTYPE: GH!; Isotypes: NY!, US [photo, RM!]). *Aster tanacetifolia* Kunth var. *pygmaeus* (A. Gray) A. Gray, *Syn. Fl. N. Amer.* 1(2):206. 1884. *Machaeranthera pygmaea* (A. Gray) Wootton & Standley, *Contr. U.S. Natl. Herb.* 16:189. 1913.

To these four species, which constituted section *Arida* sensu Hartman (1976), I would add the following taxa which are poorly known biosystematically.

Aster blepharophyllus A. Gray, *Pl. Wright.* 2:77. 1853, non *Machaeranthera blephariphylla* (A. Gray) Shinn., *Field & Lab.* 18:38. 1950, based on *Aplopappus blephariphyllus* A. Gray. TYPE: U.S.A. New Mexico: Hidalgo Co., Las Playas Springs, 7 Oct 1851, *C. Wright 1164* (LECTOTYPE: to be designated elsewhere, GH!, MO!, NY [photo, RM!], PH [photo, RM!], US [photo, RM!]).

Nesom, *et al.* (1990) are transferring this taxon to *Machaeranthera*, providing a new name to avoid a later homonym, and designating the lectotype. This taxon is unusual as it shares several morphological features (examples noted above in the key to the subgenera and sections) with section *Blepharodon*. Likewise, restriction site analysis of chloroplast DNA by Morgan & Simpson (1990) indicate that it is a member of that section. Conversely, probing with a ribosomal DNA gene intimated that it may not be a member of section *Blepharodon*. It is possible that *Aster blepharophyllus* was formed via hybrid speciation at the diploid level between members of sections *Arida* and *Blepharodon*.

Machaeranthera carnosus (A. Gray) Nesom, *Phytologia* 67:439. 1989. BASIONYM: *Linosyris carnosus* A. Gray, *Pl. Wright.* 2:80. 1853. TYPE: MÉXICO. Sonora: "low, subsaline valley, west of Chiricahui Mountains," Sep 1851, *C. Wright 1187* (HOLOTYPE: GH; Isotypes: PH [photo, RM!], US [2 sheets; photos, RM!]). *Aster carnosus* (A. Gray) A. Gray *ex* Hemsley, *Biol. Cent.-Amer., Bot.*, 2:120. 1881, non *Aster carnosus* Gilib., *Fl. Lit. Inch.* 1:214. 1781. *Leucosyris carnosus* (A. Gray) E. Greene, *Fl. Francisc.* 384. 1897.

Bigelovia intricatus A. Gray, *Proc. Amer. Acad. Arts* 17:208. 1882. TYPE: U.S.A. California: Mohave Desert, at Lancaster Station, *C.C. Parry s.n.* (HOLOTYPE: GH). *Aster intricatus* (A. Gray) S.F. Blake, *J. Wash. Acad. Sci.* 27:378. 1937.

Nesom (1989) transferred this taxon to *Machaeranthera* on account of its similarities to *M. riparia* and *Aster blepharophyllus*. I suggested this disposition following the rediscovery of *A. blepharophyllus* after observing the strong resemblance among these three species. Previously it had been treated by Sundberg (1986) as *Leucosyris carnosus*.

Machaeranthera riparia (Kunth) A.G. Jones, Syst. Bot. 8:85. 1983.
 BASIONYM: *Aster riparius* Kunth, Nov. Gen. Sp. 4:92. 1820.
 TYPE: MÉXICO: A.J.A. Bonpland 4308 (HOLOTYPE: P [photo, RM!]; Isotypes B, MSC).

Aster sonorae A. Gray, Smithsonian Contr. Knowl. 5(6):76. 1853.
 TYPE: U.S.A. "S. Arizona, west of the Chiricahua Mountains,"
 Sep 1851, C. Wright 1169 (HOLOTYPE: GH!; Isotypes: CGE,
 PH [photo, RM!], US [photo, RM!]). *Machaeranthera sonorae*
 (A. Gray) Stucky, Amer. J. Bot. 65:132. 1978.

This species hybridizes naturally with *M. parviflora* along the margin of Lordsburg Playa near Lordsburg, Hidalgo Co., New Mexico (Hartman, pers. observ.; W.L. Wagner, pers. comm., Wagner 3457, 3461). The two taxa also were successfully crossed artificially by Stucky & Jackson (1975).

Machaeranthera turneri Arnold & R. Jackson, Syst. Bot. 3:209. 1978.
 TYPE: MÉXICO. Chihuahua: 5.4 km N of Meoqui, along hwy. 45,
 1 Aug 1964, R.C. Jackson 4005 (HOLOTYPE: TTC).

Hartman (1976) noted that plants of *Machaeranthera parviflora* from W Texas, S New Mexico, and S Arizona are fairly uniform with receptacles (measured after achenes have fallen and phyllaries are reflexed) 2-3 mm in diameter, pappus of ray florets about half the length that of disc florets, and phyllaries with appressed apices. But these features show a clinal change with populations in the southern portion of the range (W central Coahuila and E central Chihuahua) having receptacles 8-11 mm in diameter, pappi often of nearly equal lengths on ray and disc florets, and squarrose phyllaries. The southern populations would represent *M. turneri*. A more detailed study with intensive fieldwork is needed to determine whether these two names indeed apply to extremes of a cline or whether they represent good species.

5. *Machaeranthera* section *Psilactis* (A. Gray) B. Turner & D. Horne, Brittonia 16:321. 1964. BASIONYM: *Psilactis* A. Gray, Mem. Amer. Acad. Arts, ser. 2, 4:71. 1849. TYPE SPECIES: *Psilactis asteroides* A. Gray, Mem. Amer. Acad. Arts, ser. 2, 4:72. 1849 (\equiv *Machaeranthera boltoniae* [E. Greene] B. Turner & D. Horne), non *Machaeranthera asteroides* (Torrey) E. Greene, Pittonia 3:63. 1892.

Plants taprooted annuals to short lived perennials (rhizomatous with fibrous roots and stoloniform offsets in *Machaeranthera odysseus*), 3-11 dm tall.

Leaves entire, rarely coarsely serrate (the short-persisting lower cauline and especially basal leaves often toothed to shallowly pinnatifid). Heads radiate. Involucre broadly turbinate to hemispheric. Phyllaries often stipitate glandular, in 2-4 series of nearly equal length or slightly graduated, linear to narrowly lanceolate, green and herbaceous throughout or, especially in inner series, with stiff, white to stramineous margins in lower third, apices erect, obtuse to acute or short acuminate. Receptacles indistinctly alveolate, without scales. Ray florets white to blue or violet. Achenes essentially monomorphic, 1-2 mm long (dimorphic in *M. heterocarpa*, disc achenes to 2.9 mm long), oblong or narrowly obovate, only slightly flattened laterally, walls thin with 4-10 filiform nerves (14-18 ribs in *M. heterocarpa*), moderately pubescent or glabrous. Pappus of ray florets absent, of disc florets 2-4 mm long, white bristles filiform, not basally flattened, apparently in one series. Chromosome number, $n = 3, 4, \text{ or } 9$.

The following key is based in part on data from Hartman & Lane (1987), Nesom (1990), Turner (1972), and Turner & Horne (1964). At the time this manuscript was being completed, I had only a limited selection of specimens of these taxa available for study. The remainder were on loan to TEX/LL where David Morgan was completing a detailed study of this section.

1. Ligules of ray florets 2.5-4.0 mm long; involucre 2.4-4.0 mm tall, 3-4 mm wide *M. brevilingulata*
- 1' Ligules of ray florets 5-14 mm long; involucre (4-)5-10 mm tall, 5-20 mm wide
2. Plants rhizomatous with fibrous roots and stolon like offsets; stems monocephalous; basal leaves entire *M. odysseus*
- 2' Plants taprooted; stems usually all erect, with few to many heads; basal leaves, if present, entire or commonly toothed
3. Involucre broadly turbinate, 5-7 mm wide, enclosing 30-75(-90) florets, phyllaries 0.5-0.7 mm wide
4. Plants biennial or short lived perennial; base of cauline leaves mostly rounded to auriculate clasping; disc achenes thinly puberulent, fusiform to oblanceoloid, 1.4-2.0(-2.2) mm long, 7-9 ribbed; restricted to W Texas and N México
- 4' Plants annual; base of cauline leaves slightly, if at all, tapered; disc achenes glabrous or essentially so, irregularly oblanceoloid, 2.5-2.9 mm long, 14-18 ribbed; restricted to gulf coastal Texas
- 3' Involucre hemispheric, 6-20 mm wide, enclosing 75-200 florets, phyllaries 0.75-2.10 mm wide

5. Ligules of ray florets 5-7 mm long, 0.8-1.0 mm wide, uppermost leaves not markedly ampliate at the base; lower leaves and stem pubescent with short, appressed, eglandular hairs *M. boltoniae*
- 5' Ligules of ray florets (6-)7-14 mm long, 1.0-1.8 mm wide; uppermost leaves markedly ampliate at base; lower leaves and stem pubescent with glandular hairs 6.
6. Uppermost leaves narrowly ampliate, scarcely cordate; involucre 10-14 mm wide, phyllaries 4-6 mm long; disc corollas 3.2-4.2 mm long; pappus 2.6-3.2 mm long *M. mexicana*
- 6' Uppermost leaves broadly ampliate, nearly cordate; involucre 16-20 mm wide, phyllaries 6-8 mm long; disc corollas 4.5-5.0 mm long; pappus 4.0-4.5 mm long *M. gentryi*

Species retained in this section *sensu* Turner & Horne (1964) are listed below. See that publication for complete synonymy.

Machaeranthera boltoniae (E. Greene) B. Turner & D. Horne, *Brittonia* 16:328. 1964. BASIONYM: *Aster boltoniae* E. Greene, *Pittonia* 3:248. 1897. TYPE: U.S.A. Texas: El Paso Co., El Paso, 12 Sep 1884, *M.E. Jones 4207* (one of two specimens cited: NDG, NY [photo, RM!]).

Machaeranthera brevilingulata (Schultz-Bip. *ex* Hemsley) B. Turner & D. Horne, *Brittonia* 16:324. 1964. BASIONYM: *Psilactis brevilingulata* Schultz-Bip. *ex* Hemsley, *Diagn. Pl. Nov. Mexic.* 2:34. 1879. TYPE: MÉXICO: about Tacubaya, Sep 1854, *W. Schaffner 211* (HOLOTYPE: K; Isotype: GH!). *Aster brevilingulatus* (Schultz-Bip. *ex* Hemsley) McVaugh, *Contr. Univ. Michigan Herb.* 9:362. 1972.

Machaeranthera gentryi (Standley) R. Jackson *ex* B. Turner, *Phytologia* 25:57. 1972. BASIONYM: *Aster gentryi* Standley, *Field Mus. Nat. Hist., Bot. Ser.* 22:60. 1940. TYPE: MÉXICO. Chihuahua: Río Mayo, Memelichi, elev. 2250 m, 15 Sep 1936, *H.S. Gentry 2728* (HOLOTYPE: F; Isotype: US!).

Machaeranthera mexicana B. Turner & D. Horne, *Brittonia* 16:330. 1964. TYPE: MÉXICO. México: ca. 35 km W of Toluca along hwy. 15, 3 Aug 1960, *R.M. King 3595* (HOLOTYPE: TEX!; Isotypes: MICH, NY! [2 sheets], US [photo, RM!]).

Machaeranthera tenuis (S. Watson) B. Turner & D. Horne, *Brittonia* 16:326. 1964. BASIONYM: *Psilactis tenuis* S. Watson, *Proc. Amer.*

Acad. Arts 26:139. 1891. TYPE: MÉXICO. Nuevo León: Sierra Madre, near Monterrey, 15 Jun 1888, *C.G. Pringle 2238* (HOLOTYPE: GH!).

To these five taxa I would add the following, which are less well known biosystematically.

Machaeranthera heterocarpa R.L. Hartman & Lane, *Brittonia* 39:253. 1987. TYPE: U.S.A. Texas: San Patricio Co., Welder Wildlife Refuge, ca. 2.4 km E of headquarters, 20 Oct 1973, *R.L. Hartman 3785* (HOLOTYPE: RM!; Isotypes: NY!, TEX!).

Machaeranthera odysseus Nesom, *Syst. Bot.* 3:218. 1978. TYPE: MÉXICO. Nuevo León: Cerro Peña Nevada, ca. 5 km NE of mountain locally known as Picacho Onofre or 35 km ENE of Doctor Arroyo, 28 Jul 1977, *G.L. Nesom R585* with C. Wells (HOLOTYPE: US [photo, RM!]; Isotypes: ENCB, GH, LL, MEXU, NCU, RM!, TTC, US! [photo, RM]).

This section is diverse chromosomally. It appears to be based on $x = 4$, as three taxa have $n = 4$. *Machaeranthera heterocarpa* with $n = 3$ is likely derived through descending aneuploidy from *M. tenuis*, the taxon with which it was long confused, or a common ancestor (Hartman & Lane 1987). There is no published chromosome count for *M. gentryi*, which is known only from the type. It is most similar to the taxa (especially *M. mexicana*) with $n = 4$. Finally, two species, *M. brevilungulata* and *M. odysseus*, appear anomalous, having a haploid number of $n = 9$. Based on general morphology and chromosome number, it is quite likely that *Aster pauciflorus* Nutt., which was treated as the sole member of *Aster* subgenus *Almutaster* by Sundberg (1986), belongs with the latter two taxa. Further study will be necessary to confirm this disposition (Semple & Hartman, unpubl.). Interestingly, *A. pauciflorus* (as *A. hydrophyllus* E. Greene) and *A. riparius* (\equiv *M. riparia*) were crossed by Stucky & Jackson (1975) to *M. parviflora* of section *Arida*. Consequently, it is possible that none of the species used in the intergeneric crossing portion of their study on DNA content and chromosome evolution in Astereae was from outside the natural circumscription of *Machaeranthera* sections *Arida* and *Psilactis* (Semple & Hartman, unpubl.).

MACHAERANTHERA Subgenus *SIDERANTHUS* (Sections 6-8)

- II. *Machaerantha* subgenus *Sideranthus* (Nutt. ex Nees) R.L. Hartman, *comb. nov.* BASIONYM: *Sideranthus* Nutt. ex Nees in Wied-Neuw., *Reise Nord-America* 2:440. 1841. *Dieteria* subgenus *Sideranthus* (Nutt. ex Nees) Nutt., *J. Acad. Nat. Sci. Philadelphia*, ser. 2, 1:177. 1848. TYPE SPECIES: *Dieteria spinulosa* (Pursh) Nutt., *Trans. Amer. Philos. Soc.*, ser. 2, 7:301. 1840 (\equiv *Machaerantha pinnatifida* [Hook.] Shinn.).

Ray florets yellow, always present.

6. *Machaerantha* section *Sideranthus* (Nutt. ex Nees) R.L. Hartman, *comb. nov.* BASIONYM: *Sideranthus* Nutt. ex Nees in Wied-Neuw., *Reise Nord-America* 2:440. 1841. TYPE SPECIES: *Dieteria spinulosa* (Pursh) Nutt. *Dieteria* section *Sideranthus* (Nutt. ex Nees) Nutt. ex Walp., *Repert. Bot. Syst.* 2:587. 1843.

Plants taprooted annuals, biennials, or perennials, sometimes with a much branched caudex, 0.3-7.0 dm tall. Leaves entire, serrate, dentate, or pinnatifid to deeply bipinnatifid, teeth or lobes usually bristle tipped, often markedly so. Heads radiate. Involucre broadly turbinate to depressed campanulate. Phyllaries in 4-8 graduated series, linear to narrowly oblong, lower portion rigid, light green to stramineous, upper half to fifth with a green patch or strip (sometimes blackish near apex), usually pubescent, often with glandular trichomes, erect to squarrose, obtuse to acuminate, usually tipped by a stiff and often pronounced bristle. Receptacles usually alveolate, scales poorly developed or to 3 mm long. Ray florets yellow. Achenes often dimorphic, 1.5-3.2 mm long, elliptic to narrowly obovate, walls thin with 6-16 nerves or weak ribs, glabrous to moderately pubescent; ray achenes usually rounded on dorsal edge, often asymmetrical, and slightly shorter; disc achenes flattened laterally. Pappus 3.5-6.0 mm long, white to tawny, bristles slightly to moderately dorsoventrally flattened basally, in 2-4 markedly graduated series; pappus of ray florets sometimes reduced in length. Chromosome number, $n = 2, 3, 4, \text{ or } 8$.

1. Plants annual with herbaceous stems; involucre eglandular2.
2. Leaves with entire margins, not bristle lined, or lower cauline and basal ones tridentate or sometimes pinnatifid; restricted to Sierra San Pedro Mártir, NE Baja California, México *M. wigginsii*
- 2' Leaves uniformly spinulose toothed or lobed, bristles usually 1.5-3.0 mm long; phyllaries (except innermost series) tipped by bristles usually 0.6-1.5 mm long; occurring elsewhere *M. gracilis*

- 1' Plants perennial, stems with woody bases; involucre glandular 3.
3. Bracts of upper peduncles imbricate and grading into phyllaries; stems nearly leafless above base *M. juncea*
- 3' Bracts few and not grading into phyllaries; stems leafy or leaves reduced near the inflorescence 4.
4. Phyllaries strongly squarrose in upper half; leaves thickish, usually oblanceolate to spatulate with bluntly dentate to subentire margins; restricted to Cape region of Baja California Sur and adjacent islands *M. arenaria*
- 4' Phyllaries with appressed to spreading apices; leaves thin, usually oblong to lanceolate with prominent teeth or lobes; found throughout much of SW Canada, W United States, and N half of México *M. pinnatifida*

This section contains five species following the transfer of *Machaeranthera heterophylla* to section *Blepharodon* (see above).

Machaeranthera arenaria (Benth.) Shinn., Field & Lab. 18:40. 1950.
 BASIONYM: *Aplopappus arenarius* Benth., Bot. Voy. Sulphur p. 24. 1844. TYPE: MÉXICO. Baja California Sur: Cabo San Lucas, 1841, R.B. Hinds s.n. (HOLOTYPE: K; Isotype: DS! as photo).

Machaeranthera gracilis (Nutt.) Shinn., Field & Lab. 18:41. 1950.
 BASIONYM: *Dieteria gracilis* Nutt., J. Acad. Nat. Sci. Philadelphia, ser. 2, 1:177. 1848, non *Aster gracilis* Nutt., Gen. N. Amer. Pl. 2:158. 1818. TYPE: U.S.A. New Mexico: near Santa Fe, W. Gambel s.n. (HOLOTYPE: GH!; Isotype: K). *Aplopappus gracilis* (Nutt.) A. Gray, Mem. Amer. Acad. Arts, ser. 2, 4:76. 1849. *Aster dieteria* Kuntze, Revis. Gen. Pl. 1:315. 1891, based on *Dieteria gracilis* Nutt. *Eriocarpum gracile* (Nutt.) E. Greene, Erythea 2:190. 1894. *Sideranthus gracilis* (Nutt.) Nelson, Bot. Gaz. (Crawfordsville) 37:266. 1904.

Haplopappus ravenii R. Jackson, Amer. J. Bot. 49:123. 1962.
 TYPE: U.S.A. Arizona: Yavapai Co., near Johnson Wash, ca. 16 km S of the Verde River, 8 Jun 1959, R.C. Jackson 2680 (HOLOTYPE: KANU!).

This species is treated in the broad sense to include the $n = 4$ *Haplopappus ravenii* in addition to the $n = 2$ and 3 chromosomal races. According to Jackson (1962; 1971), the $n = 4$ race can be distinguished from the other two on the basis of floret and phyllary morphology. The former is said to possess fewer and shorter pappus

bristles, shorter achenes, and phyllaries that are covered by stiffer and more erect trichomes. I have been unable to make this distinction with confidence. It is true that *H. ravenii* (based on specimens from its described geographic range, but not confirmed by chromosome counts) has phyllaries with trichomes which are often sparse and ascending to spreading versus more numerous, generally appressed, and longer. Unfortunately, in surveying several hundred sheets of *Machaeranthera gracilis* sensu lato, approximately twenty percent showed intermediacy in this character. Formal recognition of the $n = 4$ race has been questioned by Cronquist (1971) and others.

Machaeranthera juncea (E. Greene) Shinn., Field & Lab. 18:40. 1950. BASIONYM: *Aplopappus junceus* E. Greene, Bull. Calif. Acad. Sci. 1:190. 1885. TYPE: U.S.A. California: San Diego Co., Cleveland, M.K. Curran s.n. (HOLOTYPE: NDG). *Eriocarpum junceum* (E. Greene) E. Greene, Erythea 2:108. 1894. *Sideranthus junceus* (E. Greene) Davidson & Moxley, Fl. S. California p. 377. 1923.

Machaeranthera pinnatifida (Hook.) Shinn., Sida 1:295. 1964. BASIONYM: *Diplopappus pinnatifidus* Hook., Fl. Bor.-Amer. 2:22. 1834. TYPE: CANADA. Saskatchewan: Rocky Mountains near Jasper's Lake, T. Drummond s.n. (HOLOTYPE: K?; Isotype: NY [photo, RM!]).

For complete synonymy and a taxonomic treatment of this polymorphic species, the reader is referred to Turner & Hartman (1976). A total of seven varieties distributed between two subspecies are recognized. They often intergrade in areas of sympatry.

Machaeranthera wigginsii (S.F. Blake) R.L. Hartman, *comb. nov.* BASIONYM: *Haplopappus wigginsii* S.F. Blake, Proc. Biol. Soc. Wash. 48:169. 1935. TYPE: MÉXICO. Baja California: Sierra San Pedro Mártir, 18 Sep 1930, I.L. Wiggins & D. Demaree 4914 (HOLOTYPE: US!).

This species, which is restricted to the Sierra San Pedro Mártir of NE Baja California, is most closely related to *Machaeranthera gracilis*.

7. *Machaeranthera* section *Havardii* (R. Jackson) R.L. Hartman, *comb. nov.* BASIONYM: *Haplopappus* section *Havardii* R. Jackson, Univ. Kansas Sci. Bull. 46:479. 1966. TYPE SPECIES: *Haplopappus havardii* Waterf.

Plants taprooted annuals, 1.5-4.5 dm tall. Leaves serrate or dentate, often coarsely so, teeth blunt or terminating in stiff callosities, not bristle tipped. Heads radiate. Involucre broadly turbinate. Phyllaries in 5-7 graduated series, linear to narrowly oblong, lower portion rigid, stramineous, upper fifth to half with green patch or strip, densely glandular, erect, obtuse to acute. Receptacles alveolate, with scales to 0.4 mm long. Ray florets yellow. Achenes essentially monomorphic, 2.5-3.0 mm long, oblong or narrowly elliptic, sometimes slightly asymmetrical, flattened laterally, walls thin with 12-14 nerves, sparsely pubescent. Pappus similar in ray and disc florets, 5-7 mm long, white, bristles filiform, not basally flattened, in 2-3 poorly defined series. Chromosome number, $n = 4$.

Machaeranthera viscida (Wooton & Standley) R.L. Hartman, *comb. nov.* BASIONYM: *Sideranthus viscidus* Wooton & Standley, Contr. U.S. Natl. Herb. 16:180. 1913. TYPE: U.S.A. New Mexico: Eddy Co., near Hope, 3 Aug 1905, *E.O. Wooton s.n.* (HOLOTYPE: US [photo, RM!]). *Haplopappus viscidus* (Wooton & Standley) S.F. Blake, J. Wash. Acad. Sci. 28:486. 1938.

Haplopappus havardii Waterf., Rhodora 45:352. 1943. TYPE: U.S.A. Texas: Culberson Co., 13.6 km E Van Horn, *U.T. Waterfall 4159* (HOLOTYPE: GH; Isotypes: ARIZ!, MO, NY!).
Machaeranthera havardii (Waterf.) Shinn., Field & Lab. 18:40. 1950.

A species restricted to Chaves, Eddy, and Lea counties, New Mexico and Culberson, Ector, and Hudspeth counties, Texas. Until recently (Jackson 1969) it was usually called *Machaeranthera havardii* (or *Haplopappus havardii*) but this name is a synonym of *M. viscida*, an earlier name that had been "misplaced" in synonymy under the very different *H. spinulosus* (\equiv *M. pinnatifida*) by Hall (1928).

8. *Machaeranthera* section *Stenoloba* R.L. Hartman, *sect. nov.* TYPE SPECIES: *Machaeranthera stenoloba* (E. Greene) Shinn.

A *Machaeranthera* section *Sideranthus* achaeniis disci late obovatis vel leviter angustaque cordatis parietibus crassis costis prominentibus in quoque facie 5-6, dense pubescentibus marginibus incrassatis, pappo 2-3 mm longis pro parte maxima setis subulatis valde dorsiventraliter complanatus.

Plants taprooted annuals or possibly biennials, (1-)2-4 dm tall. Leaves deeply pinnatifid with linear to subulate lobes tipped by weak seta, often

bipinnatifid on lower part of plant. Heads radiate. Involucre depressed hemispheric. Phyllaries in 4-5 weakly graduated series, narrowly to broadly linear, lower portion rigid, stramineous, with a midline, upper half to two-thirds green or purple tinged, densely stipitate glandular, spreading to reflexed, long attenuate. Receptacles alveolate, with scales less than 0.2 mm long. Ray florets yellow. Achenes dimorphic, ca. 2.5-3.0 mm long, broadly obovate to obscurely and narrowly cordate, usually symmetrical, walls thick, with 10-12 prominent ribs, densely pubescent, margins markedly thickened; ray achenes wedge shaped in cross section; disc achenes compressed laterally. Pappus similar in ray and disc florets, 2-3 mm long, tawny, bristles subulate to filiform, in 3-5 graduated series, markedly dorsiventrally flattened basally. Chromosome number, $n = 4$ (Ralston, *et al.* 1989; G. Brown, unpubl.).

Machaeranthera stenoloba (E. Greene) Shinn., *Field & Lab.* 18:40. 1950. BASIONYM: *Eriocarpum stenolobum* E. Greene, *Erythea* 2:109. 1894. TYPE: MÉXICO. Chihuahua: Sierra Madre, sandy flats, Arroyo Ancho, 16 Oct 1887, *C.G. Pringle 1903* (HOLOTYPE: NDG; Isotypes: GH!, NY!, PH!). *Haplopappus stenolobus* (E. Greene) H.M. Hall, *Publ. Carnegie Inst. Wash.* 389:65. 1928.

Aplopappus tenuilobus A. Gray *ex* E. Greene, *Erythea* 2:109. 1894, *pro syn.*, *non* A. Gray, *Proc. Amer. Acad. Arts* 21:385,432. 1886.

This very distinctive and showy species is restricted to the mountains of SW Chihuahua, México, having been collected only a few times and apparently rare (G.L. Nesom, pers. comm.).

EXCLUDED SPECIES

Haplopappus brickellioides S.F. Blake, *Proc. Biol. Soc. Wash.* 35:173. 1922. Type: U.S.A. Nevada: Nye Co., Sheep Mountain, Ash Meadows, May-Oct 1898, *J.A. Purpus 6022* (HOLOTYPE: US [photo, RM!]; Isotypes: NY [photo, RM!], UC!).

Hall (1928) included this species in *Haplopappus* section *Blepharodon*, but Jackson (1968) has shown that its affinities are with *Haplopappus* section *Hazardia* or the genus *Hazardia* (Clark 1979).

Machaeranthera aurea (A. Gray) Shinn., *Field & Lab.* 18:41. 1950. \equiv *Haplopappus aureus* A. Gray, *Mem. Amer. Acad. Arts*, ser. 2, 4:76. 1849. Type: U.S.A. Texas: Harris Co.?, low prairies near Houston, Sep-Oct, *C. Wright s.n.* (HOLOTYPE: GH!; Isotypes: PH!, US!).

This species is a member of the "Phyllocephalus" group of *Haplopappus*; see discussion below.

Machaeranthera annua (Rydb.) Shinn., *Sida* 1:378. 1964. \equiv *Haplopappus annuus* (Rydb.) Cory, *Rhodora* 38:407. 1936. BASIONYM: *Sideranthus annuus* Rydb., *Bull. Torrey Bot. Club* 31:653. 1904, new name for *Aplopappus rubiginosus* Torrey & A. Gray in A. Gray, *Syn. Fl. N. Amer.* 1(2):130. 1884, non Torrey & A. Gray, *Fl. N. Amer.* 2:240. 1842. TYPE: U.S.A. Texas: *T. Drummond 110* (HOLOTYPE: GH; Isotype: NY [photo, RM!]).

This species is a member of the "Phyllocephalus" group of *Haplopappus*; see discussion below.

Machaeranthera kingii (D. Eaton) Cronq. & Keck, *Brittonia* 9:239. 1957. \equiv *Aster kingii* D. Eaton, *Botany Fortieth Parallel* 5:141,142, pl. 16. 1871. TYPE: U.S.A. Utah: above Cottonwood Canyon, Wasatch Mountains, 2748 m, Aug 1869, *S. Watson 507* (HOLOTYPE: YU?; Isotypes: NY [photo, RM!], US [photo, RM!]).

Machaeranthera kingii (D. Eaton) Cronq. & Keck var. *barnebyana* Welsh & Goodrich, *Brittonia* 33:299,300. 1981. \equiv *Aster kingii* D. Eaton. TYPE: U.S.A. Utah: Millard Co., Canyon Mountains, Eightmile Creek, 11 km WNW from Scipio, 2350 m, 12 Aug 1980, *S. Goodrich 14929* (HOLOTYPE: BRY; Isotypes: GH, NY, RM!, UC, US [photo, RM!], USFS!, UT, UTC).

Machaeranthera cognata (H.M. Hall) Cronq. & Keck, *Brittonia* 9:239. 1957. \equiv *Xylorhiza cognata* (H.M. Hall) T.J. Watson (see Watson 1977, for a revision of *Xylorhiza*).

Machaeranthera frutescens (S. Watson) Cronq. & Keck, *Brittonia* 9:239. 1957. \equiv *Xylorhiza frutescens* (S. Watson) E. Greene, *Pittonia* 3:48. 1896 (see Watson 1977).

Machaeranthera glabriuscula (Nutt.) Cronq. & Keck, *Brittonia* 9:239. 1957. \equiv *Xylorhiza glabriuscula* Nutt., *Trans. Amer. Philos. Soc.*, ser. 2, 7:297. 1840 (see Watson 1977).

Machaeranthera glabriuscula (Nutt.) Cronq. & Keck var. *confertifolia* Cronq., *Leaf. W. Bot.* 10:11. 1963. \equiv *Xylorhiza confertifolia* (Cronq.) T.J. Watson (see Watson 1977).

Machaeranthera glabriuscula (Nutt.) Cronq. & Keck var. *villosa* (Nutt.) Cronq. & Keck, *Brittonia* 9:239. 1957. \equiv *Xylorhiza glabriuscula* Nutt. var. *glabriuscula* (see Watson 1977).

Machaeranthera orcuttii (Vasey & Rose) Cronq. & Keck, *Brittonia* 9:239. 1957. \equiv *Xylorhiza orcuttii* (Vasey & Rose) E. Greene, *Pittonia* 3:48. 1896 (see Watson 1977).

Machaeranthera phyllocephala (DC.) Shinn., *Field & Lab.* 18:40. 1950. \equiv *Haplopappus phyllocephalus* DC., *Prodr.* 5:347. 1936. TYPE: MÉXICO. Tamaulipas: between San Fernando and Matamoros, 1832, *J.L. Berlandier* 2278 (HOLOTYPE: G [photo, RM!]; Isotypes: G, K, NY [photo, RM!]).

This species is a member of the "Phyllocephalus" group of *Haplopappus*; see discussion below.

Machaeranthera phyllocephala (DC.) Shinn. var. *megacephala* (Nash) Shinn., *Field & Lab.* 18:40. 1960. \equiv *Haplopappus phyllocephalus* DC. BASIONYM: *Eriocarpum megacephalum* Nash, *Bull. Torrey Bot. Club* 23:107. 1896. TYPE: U.S.A. Florida: Manatee Co., S shore of Sneed's Island, near mouth of Manatee River, 21-23 Aug 1895, *G.V. Nash* 2492 (HOLOTYPE: NY!: Isotypes: G, GH, K, NDG, PH [photo, RM!], US [photo, RM!]).

This species is a member of the "Phyllocephalus" group of *Haplopappus*; see discussion below.

Machaeranthera tortifolia (Torrey & A. Gray) Cronq. & Keck, *Brittonia* 9:239. 1957. \equiv *Xylorhiza tortifolia* (Torrey & A. Gray) E. Greene, *Pittonia* 3:48. 1896 (see Watson 1977).

Machaeranthera tortifolia (Torrey & A. Gray) Cronq. & Keck var. *imberbis* Cronq., *Leaf. W. Bot.* 10:12. 1963. \equiv *Xylorhiza tortifolia* (Torrey & A. Gray) E. Greene var. *imberbis* (Cronq.) T.J. Watson (see Watson 1977).

Machaeranthera venusta (M.E. Jones) Cronq. & Keck, *Brittonia* 9:239. 1957. \equiv *Xylorhiza venusta* (M.E. Jones) A.A. Heller, *Muhlenbergia* 1:8. 1900 (see Watson 1977).

Machaeranthera wrightii (A. Gray) Cronq. & Keck, *Brittonia* 9:239. 1957. \equiv *Xylorhiza wrightii* (A. Gray) E. Greene, *Pittonia* 3:47. 1896 (see Watson 1977).

The "Phyllocephalus" group of *Haplopappus* currently is under study by Hartman and Lane (Hartman & Lane 1984; Lane & Hartman 1984; Lane & Hartman 1985; Lane, *et al.* 1987). It is part of an $x = 6$ chromosomal line which includes *Isocoma*, *Stephanodoria*, *Grindelia*, *Xanthocephalum*, *Olivaea*, *Prionopsis*, probably *Pyrocoma* and *Oonopsis*, and perhaps *Xylorhiza*. In addition to the common chromosomal base, most of these genera share a

suite of characters including goblet shaped disc corollas, deltate style branch appendages, and corolla epidermal cells that are only 3 to 4 times longer than wide and have broad longitudinal ridges and transverse endwalls. The relationship of a subset of these genera is supported by a recent analysis of chloroplast DNA restriction site mutations (Nesom, *et al.* 1990). Furthermore, hybridization studies by Jackson & Dimas (1981) indicate that the "Phyllocephalus" group is closely related to, if not congeneric with, *Isocoma* (or *Haplopappus* section *Isocoma*).

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